NITROGEN TURNOVER BY A WOODLAND POPULATION OF *LUMBRICUS TERRESTRIS*

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Introduction

Recent reviews (SATCHELL, 1958, 1960; RAW, 1961) have suggested that the amounts of readily mineralised nitrogen released by earthworms may be large compared with the nitrogen requirements of crops. This paper presents some biomass estimates for a woodland population of *Lumbricus terrestris*, a provisional estimate of its rate of tissue production determined by Mr. J. G. Skellam of the Nature Conservancy, London, and a discussion of the possible significance of these estimates in terms of nitrogen flow through the population.

Site

The site, Merlewood Lodge Wood, is on deep base-rich glacial drift overlying Carboniferous limestone in the grounds of Merlewood Research Station. It carries a dense stand of coppiced hazel (*Corylus*), ash *(Fraxinus)* and sycamore *(Acer)* and has a luxuriant ground flora with *Allium ursinum* dominant. Rainfall is approximately 47″ (109 cm) per annum and soil temperatures at 10 cm during 1960 were between 3.2 °C and 13.8°C.

Estimation of biomass

Formaldehyde solution was used as an earthworm expellant (RAW, 1959). Two gallons (approx. 9 litres) of water containing 50 ml of formaldehyde were applied to each sample unit of 0.5 m^2. A second application was made after 10 minutes and a third after 20 minutes. The worms were collected for 30 minutes following the first application. Five units were sampled each week during January and February 1960 and each fortnight for the remainder of the year. On each occasion soil temperature was recorded at 10 cm and moisture content was determined gravimetrically on soil cores taken to 5 cm depth.

The effect of soil moisture on the population estimates obtained during the period of study was not found to be statistically significant. The effect of soil temperature was highly significant and an elaborate regression analysis (SKELLAM, pers. com.) using running means to eliminate the effects of population change indicated an optimal value for earthworm extraction of about 10.5° C. On the basis of the Merlewood Lodge Wood samples and data from two similar sites sampled in 1961 the following correction term was obtained:

Estimated Biomass = Observed Biomass $\times$ exp. $\{.01 \quad (t - 10.5)^2\}$ where t = soil temperature at 10 cm in °C and exp.$\{x\} = e^x$, the exponential function.

The correction term is intended as a first approximation for the range of temperature encountered, namely 0.8 — 15.8°C.

Biomass estimates for the Merlewood Lodge Wood population are given in Fig. 1.

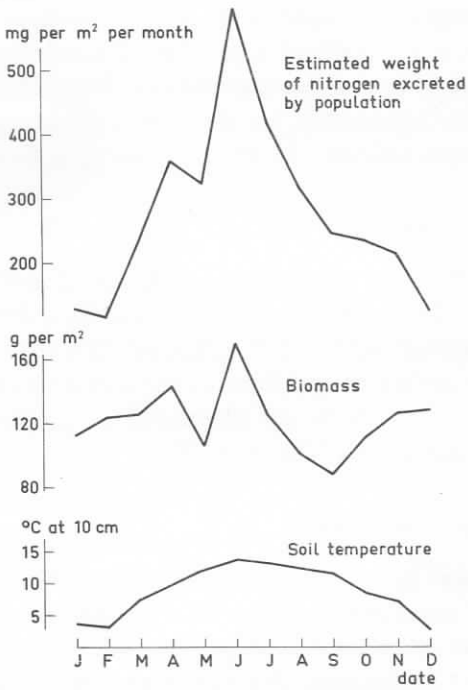

Fig. 1. Estimated weight of nitrogen excreted by a population of *Lumbricus terrestris* at Merlewood Lodge Wood in 1960.

Estimation of rate of return of dead tissue

On steady state assumptions, the rate of return of earthworm tissue to the soil, using 'soil' to include its biological constituents, may be taken as that

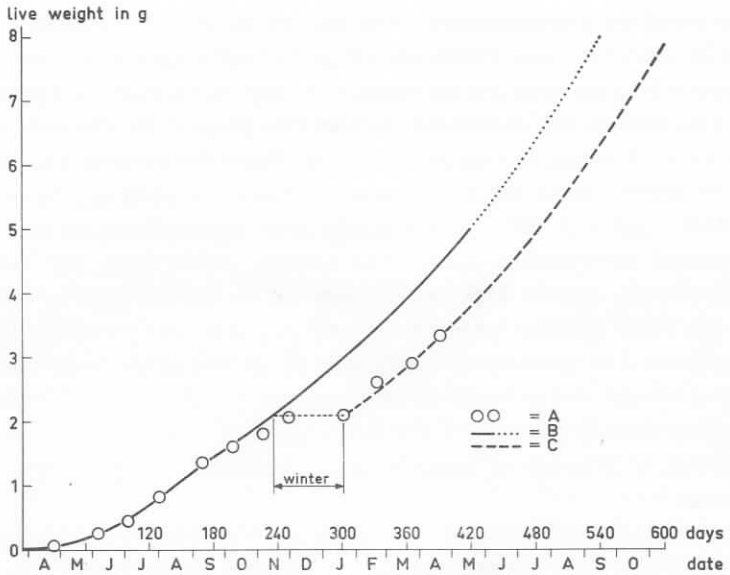

Fig. 2. Growth curves of *Lumbricus terrestris*.
A. Growth of mean weight of 27 individuals.
B. Curve based on analysis of logarithmic growth rate of a wider sample.
C. Same curve as B, displaced in time.

of its production. A method was sought therefore of estimating the production per day of earthworm tissue and its relation to the prevailing biomas or 'standing crop'. The mathematical arguments involved were kindly supplied by Mr. J. G. Skellam and the computations by Mr. K. H. Lakhani, both of the Biometrics Section of the Nature Conservancy. The estimate obtained is based on (1) the biomass estimates given above, (2) the size structure of the same population, obtained by weighing individually all the worms collected during the year's sampling and (3) data on weight increments of worms reared in a plot adjacent to the Lodge Wood obtained as follows.

One hundred and eighty specimens of various sizes up to 10 g fresh weight were weighed and placed in nylon bags containing sterilized soil and mixed deciduous leaf litter. The bags were then partly buried so that the litter layer was level with the soil surface. The worms were re-weighed after six weeks. The experiment was set up in April 1961 and 45 of the worms which were then newly hatched were subsequently re-weighed and fed at approximately monthly intervals, 27 of them surviving to the present time (April 1962).

Fig. 2 presents growth data for these 27 specimens together with a growth

curve based on a combination of all the rearing data. It is likely that this curve is similar to those which prevail in the field since it is supported independently by a study of the progression through the seasons of a peak in the size structure of the woodland populations created by the concentrated emergence of young worms in the spring. From the average size structure and the growth curve the age structure of the population can be estimated and from this it is possible, on steady state assumptions, to construct a provisional survivorship curve. The average productivity per individual recruit per day and the expected biomass per recruit can then be calculated and the ratio between productivity per day and the prevailing biomass determined. The procedure, which will be published in detail elsewhere, yields a provisional estimate of turnover rate per day per unit of biomass prevailing (standing crop) of the order of .008. For the whole year this represents a turnover of roughly three times the average weight of the biomass.

The mean of the monthly biomass estimates from Merlewood Lodge Wood was 121.4 g/m^2. The annual turnover of biomass on the basis of the above calculation would therefore approximate to 364 g/m^2.

Estimation of nitrogen turnover

The nitrogen content of *L. terrestris*, kindly determined by Mr. S. E. Allen of Merlewood Research Station, on a sample of 10 specimens taken from Merlewood Lodge Wood, was 1.75 % of the fresh weight. The annual output of nitrogen by the population in dead tissue would therefore be of the order of 6—7 g/m^2.

The mean rate of nitrogen excretion by *L. terrestris* at 23 °C was determined by NEEDHAM (1957) as 269 μg/g/day. The effect of temperature on nitrogen excretion in earthworms is unknown but it seems reasonable to suppose that it is similar to that on respiration. In *L. terrestris* this is of the normal poikilotherm type fitting the standard Krogh curve (POMERAT and ZARROW, 1936). If the Krogh curve is accepted as a basis for temperature correction it is possible to compute a provisional estimate of the output of excreted nitrogen from the population on the basis of Needham's figure, the biomass estimates and the recorded soil temperatures. From the monthly estimates shown in Fig. 1 an estimate for the annual output of 3.3. g/m^2 is obtained.

Combining these two estimates of nitrogen returned in dead tissue and

excreted nitrogen we reach an overall estimate of nitrogen turnover by the population of approximately 100 kg/ha in one year. This was from *L. terrestris* alone. The biomass of other earthworm species, of which an unknown proportion was expelled by the formaldehyde treatment was at least one fifth of the *terrestris* biomass.

Conclusions

The nitrogen content of the annual leaf fall in European woodlands is generally of the order of 30—70 kg/ha. The weight of ground flora returned annually as litter has rarely been recorded but WITKAMP and VAN DER DRIFT's (1961) figure of 83 g/m^2 for a calcareous mull suggests an additional nitrogen return from this source of probably not more than a few tens of kilograms/hectare. If the estimates quoted are even approximately correct they suggest that the nitrogen demand of the earthworm population is at least equivalent to and possibly in excess of the supply from the litter. Litter is not, of course, the only source of food nitrogen for *L. terrestris* but, when the demands of other species are taken into account, the magnitude of the estimate gives some indication of the probably intense competition for food amongst the soil fauna.

OVINGTON (1957) gives estimates of the average annual nitrogen retention by young plantations of *Pseudotsuga taxifolia*, *Pinus nigra*, *Quercus petraea* and *Betula alba* of 38, 20, 14 and 10 kg/ha respectively. The return of nitrogen to the ecosystem by the earthworm population studied appears to be several times larger than the nitrogen retention of the trees.

Acknowledgment

I should like to thank Mr. J. G. Skellam for permitting me to refer to his unpublished work from which the estimate of biomass turnover in this paper is derived and for the many helpful and stimulating ideas contributed in frequent discussions of this problem during the last two years.

Summary

The turnover of nitrogen by *L. terrestris* in a woodland site in one year is estimated as of the order of 100 kg/ha.

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Discussion

G. W. HEATH: I have made similar calculations for N-turnover by earthworms in pasture, but the results obtained when Needham's data for N-excretion are used are 12 times greater than when data are used by COHEN and LEWIS (J. Biol. Chem., **180**, 79—91 and **184**, 479—84). Is it possible that this difference arises because the latter workers used fresh worms at 8—12° C whilst Needham did his experiments at 23° C.
J. E. SATCHELL: Cohen and Lewis did not take account of the ammonium adsorbed on the faeces (v. BORLEY and JENNINGS, 1959, Austr. J. Agr. Res., **10**, 367).
G. MINDERMAN: Is it correct to estimate the competition for N by comparing the annual N-turnover of *L. terrestris* with the N-content in the annual litter supply? I consider that the annual animal N-turnover should be compared with the total amount of organic-N, present in the soil, which may be 20 or more times the annual supply.
J. E. SATCHELL: I referred to the nitrogen in the litter fall to illustrate the amount of nitrogen circulating in the ecosystem. I concluded that litter is not the only source of food nitrogen for *L. terrestris*. Konopacki obtained a respiration quotient of 0.78 for this species which suggests a protein-rich food source such as microbial protoplasm.
A. E. APINIS: Various workers have shown that the N-turnover in different forest types can differ greatly.
G. W. HARMSEN: The nitrogen mineralised from decaying dead worms may not immediately become available to the plants. A part may be directly refixed either in microbes or in humus synthesis.
J. A. VAN RHEE: From the first graph of Fig. 1 of the nitrogen excreted, we might expect a correlation with the nitrate content of the soil. Have you checked this in your field observations?
J. E. SATCHELL: No, but with a high C/N ration in the plant litter, I would not expect a correlation.
J. DOEKSEN: Earthworms kept at 23° C are absolutely abnormal and may not be taken as a base for calculations of nitrogen-turnover by earthworms.
J. E. SATCHELL: Needham's experiments lasted 15 days. The worms fed and maintained their body-weight, and excreted urea and ammonia in the normal proportions. The respiration rate of *L. terrestris* at 23° C (KONOPACKI) is related to that at lower temperatures by the normal Krogh-curve. I know no evidence for Dr. Doeksen's statements.
G. W. HEATH: It is important to consider how much of the mineralisable N from worms is released at a time crop plants can utilise it.

When pastures are ploughed out, the mineralisable N from worms is about half that present in the soil and there is a crop response to added N. Therefore I consider that in

agricultural soils the mineralisable N supplied by worms cannot be so great as Dr. Satchell suggests.

J. E. SATCHELL: Fig. 1 in my paper suggests, that the role of nitrogen excretion was highest during the growing season from April—June.